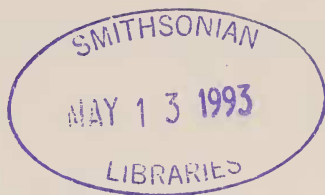


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OF THE SOUTH AFRICAN
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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* 74 (33): 627–634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) 2 (17): 309–320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* 17 (4): 1–51.

THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* 4 (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 16: 269–270.

(continued inside back cover)

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HOW MANY SPECIES OF *DIICTODON*
WERE THERE?

By

GILLIAN M. KING

Cape Town

Kaapstad

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HOW MANY SPECIES OF *DIICTODON* WERE THERE?

By

GILLIAN M. KING

Department of Karoo Palaeontology, South African Museum, Cape Town

(With 3 figures and 1 table)

[MS accepted 26 October 1992]

ABSTRACT

Twenty species of the dicynodont genus *Diictodon* have been described. Although the genus is distinguishable by reliable characters, the validity of the species-level taxonomy is questionable. The present work re-evaluates the existing species and concludes that previous authors have not been able to produce convincing species-level characters. A sample of well-preserved and well-prepared skulls in the South African Museum is used to search for any other possible species-specific characters, but none is found.

It is concluded that only one species of the genus, *Diictodon galeops*, is justifiable. The specific longevity of this dicynodont is noted.

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INTRODUCTION

The dicynodont genus *Diictodon* is distinctive and well-characterized. Descriptions of the genus have been given by Cluver & Hotton (1981), Cluver & King (1983) and King (1988). The most distinctive feature of the skull is the prominent maxillary caniniform process that is clearly demarcated from the anterior palatal rim by a deep notch (Figs 1, 2B). This feature is found in conjunction with small palatines that do not meet the premaxilla on the palatal surface, a narrow intertemporal region in which the postorbitals tend to cover the parietals (Fig. 2), prominent dentary tables of which the medial edge stands proud as a ridge, and a weakly-developed lateral dentary shelf (Fig. 3). This suite of characters permits easy identification of members of the genus.

Diictodon seems to have been a common element in the Karoo palaeoenvironment. Many specimens of the genus are known (Smith 1980), together with trackways and burrows that are probably attributable to this form (Smith 1987). Excellent postcranial material is also available. Despite this, no detailed functional study of the genus has been made, nor has a species-level revision of the taxonomy of the genus been carried out.

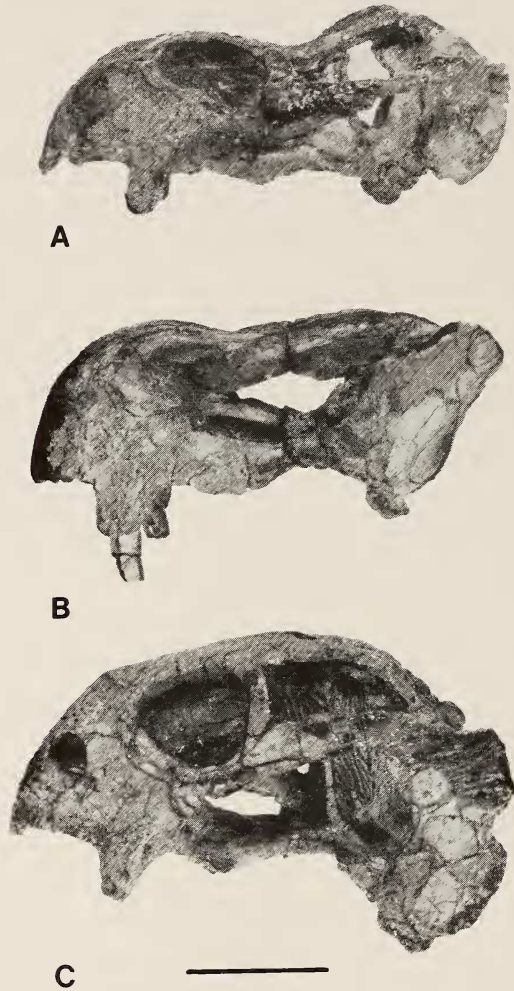


Fig. 1. Three specimens of *Diictodon* in lateral view to show the distinctive square-cut caniniform process. A. SAM-10086. B. SAM-K5105. C. SAM-K7730. Scale = 30 mm.

Owing to the wealth of material available, *Diictodon* offers an opportunity to examine the effects of intraspecific variation in a fossil species and detailed studies of this aspect of the genus are in progress (King in prep.). Stratigraphic information for specimens from the South African Karoo Basin is also available and becoming increasingly refined (Kitching 1977; Keyser & Smith 1978; Rubidge in press), so the genus also offers the possibility of studying changes in osteological morphology in time and space.

However, a prerequisite of such studies is an understanding of the species-level taxonomy of the genus. Here the existing species are reviewed and their validity, based

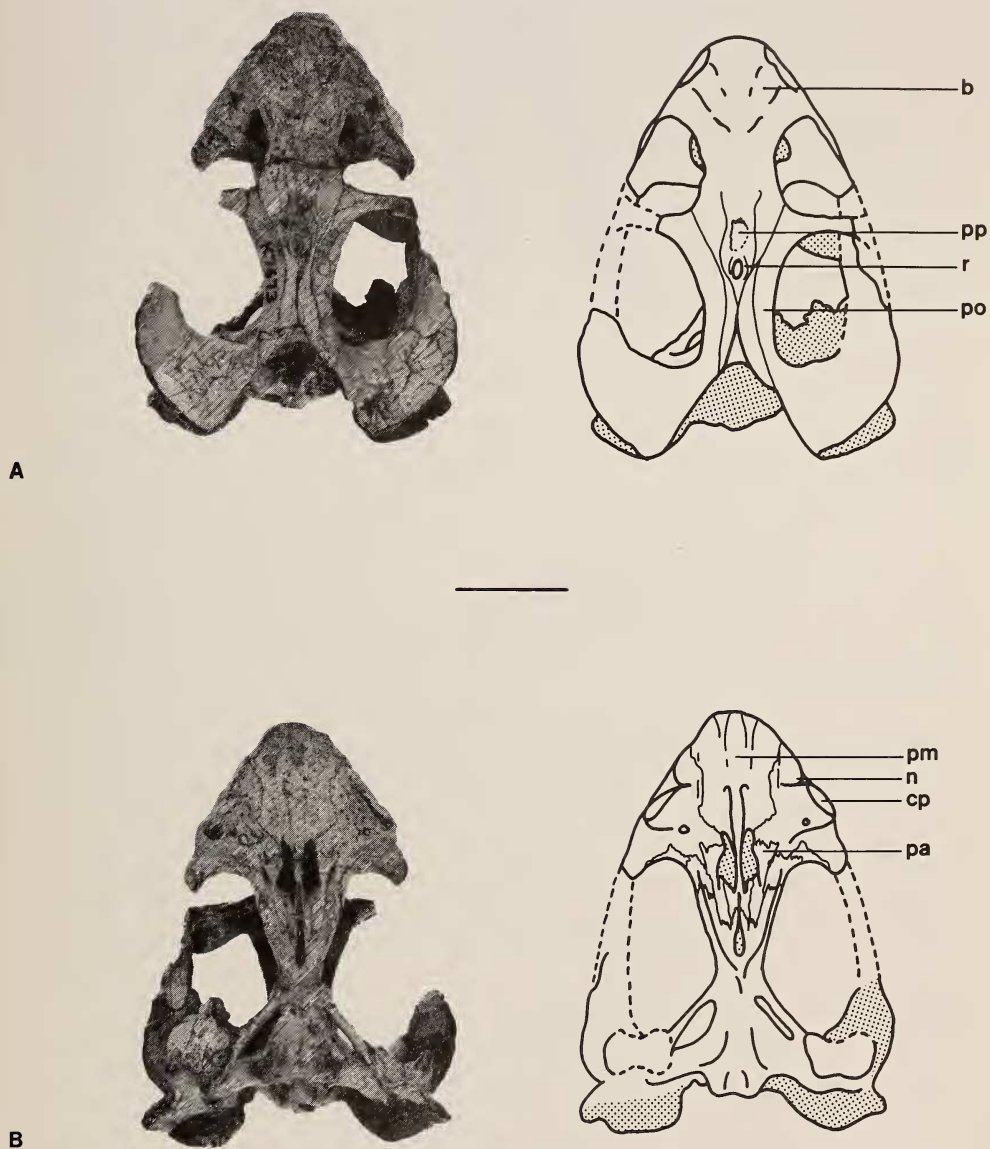


Fig. 2. *Diictodon galeops* SAM-K7673. A. Skull in dorsal view. B. Skull in palatal view. Stipple indicates area of matrix. Scale = 30 mm.

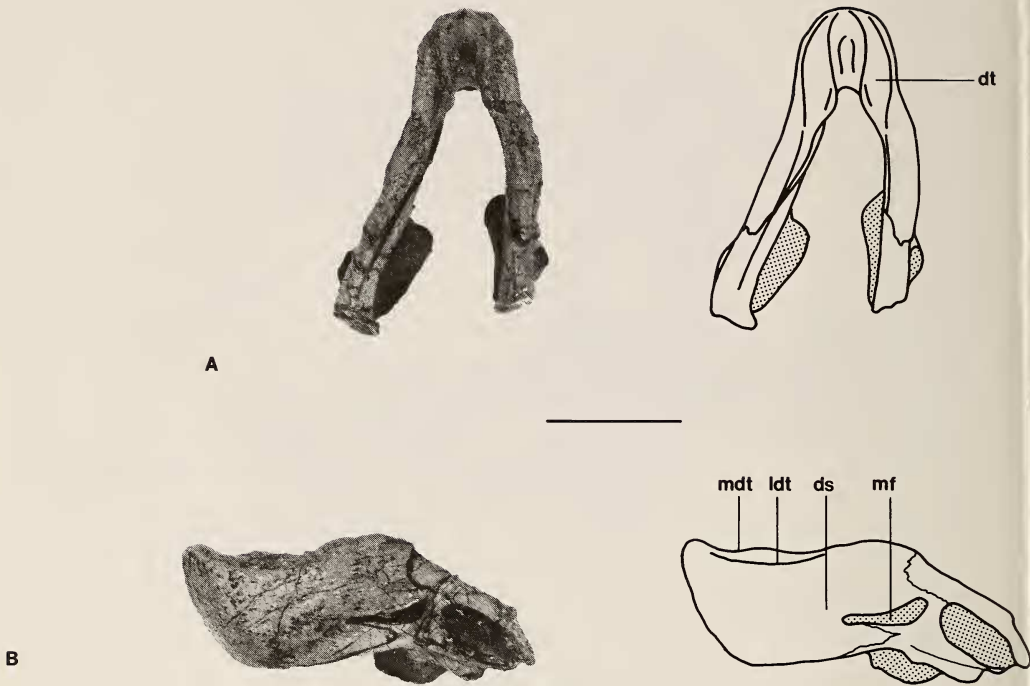


Fig. 3. *Diictodon galeops* SAM-K7730. A. Lower jaw in dorsal view. B. Lower jaw in lateral view. Stipple indicates area of matrix. Scale = 30 mm.

TABLE 1
Biostratigraphic schemes for the Karoo Sequence.

A. After Kitching (1977).

Triassic	<i>Cynognathus</i> bio-zone <i>Lystrosaurus</i> bio-zone
Permian	<i>Daptocephalus</i> bio-zone <i>Cistecephalus</i> bio-zone <i>Tapinocephalus</i> bio-zone

B. After Rubidge (in press).

Triassic	<i>Cynognathus</i> - <i>Diademodon</i> assemblage zone <i>Lystrosaurus</i> - <i>Procolophon</i> assemblage zone
Permian	<i>Dicynodon</i> - <i>Theriongnathus</i> assemblage zone <i>Cistecephalus</i> - <i>Aulacephalodon</i> assemblage zone <i>Tropidostoma</i> - <i>Endothiodon</i> assemblage zone <i>Priesterognathus</i> - <i>Diictodon</i> assemblage zone <i>Tapinocephalus</i> - <i>Bradysaurus</i> assemblage zone <i>Eodicynodon</i> - <i>Tapinocaninus</i> assemblage zone

on the characters used by the naming authors, is assessed. In addition, a collection of well-preserved and well-prepared skulls in the South African Museum is used to investigate whether there are any species-specific characters that have been missed by previous authors, and to facilitate a revision of the existing species.

Since it was hoped to draw some conclusions concerning the stratigraphic distribution of *Diictodon* species, the most refined biostratigraphic scheme for the Beaufort Sequence (Rubidge in press) has been used to assign the South African Museum sample skulls to biostratigraphic assemblage zones (see Table 1). (I am extremely grateful for the help of Dr R. M. H. Smith, South African Museum, in this regard.) However, the available locality information for the existing type specimens does not always allow assignment of those specimens to an assemblage zone in Rubidge's scheme, and their assignments to bio-zones in the previous stratigraphic scheme, as published in Kitching (1977), have been retained.

SPECIES OF *DIICTODON*

King (1988) gave a list of 20 species of the genus. Although it is clear that these forms all belong within the genus (possessing the distinctive maxillary notch and other features noted above), the validity of the species involved requires re-assessment.

The type species is *Diictodon galeops*, described by Broom (1913).

Diictodon galeops Broom, 1913

Diictodon galeops Broom, 1913: 453, fig. 15.

The type, AMNH 5308, is a skull from Slachtersnek, Somerset East District, Cape Province, South Africa. This locality is recorded as being in the *Cistecephalus* bio-zone of the Teekloof Formation, Karoo Sequence by Kitching (1977).

The feature which Broom (1913) felt distinguished this genus from the otherwise similar *Dicynodon* was the large size and peculiar shape of the preparietal. This bone surrounds the pineal opening in *Diictodon galeops*, whereas Broom considered that the usual state in *Dicynodon* was for the preparietal to lie in front of the pineal. On this basis he transferred the *Dicynodon* species *D. kolbei* and *D. alticeps* to *Diictodon*, and noted that this might also be warranted for *Dicynodon tigriceps*. However, the former two species are now regarded as belonging in the genus *Oudenodon*, and the latter in *Aulacephalodon* (King 1988).

Toerien (1953) discussed variation in the shape and position of the preparietal in *Diictodon* (*Dicynodon*) *grimbeeki* and *Diictodon sollasi*. He concluded that sutural pattern should be used as a generic or specific character only with caution, since in a sample of otherwise similar skulls from one locality, continuous variation in pattern and size of the preparietal was seen. However, Cluver & Hotton (1981) gave a revised diagnosis of the genus based on more reliable characteristics also present in the type of *Diictodon galeops*.

Of the remaining 19 species, only one, *Diictodon sesoma* Watson, 1960, was originally described as *Diictodon*, the others having been previously included in the genera *Dicynodon*, *Oudenodon* and *Emydorhynchus*.

Diictodon sesoma Watson, 1960

Diictodon sesoma Watson, 1960: 142, fig. 2.

The holotype of this species is a skull, lower jaw and postcranial skeleton from Buffel's River, Orange Free State, South Africa (UMZC R314). Watson (1960) included

it in the genus *Diictodon*, because the pineal opening is surrounded by the preparietal, but he felt that the material warranted allocation to a new species, owing to its shorter and broader skull, wider occiput, relatively wider intertemporal region, and large canine.

The intertemporal region, as illustrated by Watson, is rather wide for *Diictodon* (based on the sample of specimens in the South African Museum), although this appearance can result when the skull roof is weathered and the postorbitals obliterated. The specimen does appear to have a maxillary notch, however, although the maxillary rim in front of the tusk appears to be broken. The pineal is slightly raised above the skull roof, another feature also seen in some specimens attributed to *Diictodon*.

Diictodon feliceps (Owen, 1876)

Dicynodon feliceps Owen, 1876: 45, pl. 43.

Rhachiocephalodon feliceps (Owen, 1876) Seeley, 1898: 108.

Diictodon feliceps (Owen, 1876) Cluver & Hotton, 1981: 125.

The holotype, BMNH 47052, is from Fort Beaufort, Cape Province, South Africa (*Cistecephalus* bio-zone, Kitching 1977).

Owen (1876) felt that there was no difficulty in accommodating this specimen in the genus *Dicynodon* as then known but considered that a new species was warranted, based on skull proportion, suture pattern and curvature of the canine tusk. Owen (1876, pl. 43 (fig. 1)) showed a clear notch in front of the caniniform tusk, a characteristic indicating that the specimen can be accommodated within the genus *Diictodon*. The pinched-in nature of the temporal region, with postorbitals approaching each other over the parietals, is also typical of *Diictodon*.

Diictodon jouberti (Broom, 1905)

Dicynodon jouberti Broom, 1905: 331.

Sintocephalus jouberti (Broom, 1905) van Hoepen, 1934: 93.

Diictodon jouberti (Broom, 1905) Cluver & Hotton, 1981: 127.

The holotype skull (SAM-695) is from Gouph (Koup) Tract, Beaufort West District, South Africa. The locality is in a low to middle horizon of the *Tapinocephalus* bio-zone (Kitching 1977).

Broom (1905) considered that the noteworthy features of the skull were that the parietal, frontal and upper part of the nasal are practically in one plane; the interparietal portion is about equal in breadth to the interorbital; and the jugal arch is unusually deep in the region of the postorbital bar.

Broom (1905) described a series of skulls, some with large and others with smaller canines. He considered this to be a sexual difference, since the two forms do not differ consistently in size.

The type has a distinctly notched maxilla in front of the tusk typical of *Diictodon*.

Diictodon psittacops (Broom, 1912)

Dicynodon psittacops Broom, 1912: 869, pl. 92.

Diictodon psittacops (Broom, 1912) Cluver & Hotton, 1981: 129.

The holotype skull and skeleton (AMNH 5534) are from the Beaufort West comonage, Cape Province, South Africa. This locality is in the *Cistecephalus* bio-zone according to Kitching (1977).

Broom (1912) considered the distinguishing features of this new species to be the narrow nasals, thickened upper part of the nasals, elevated prefrontal region of the orbital margin, broad and flat frontal region, pineal foramen that is situated on an elevated preparietal, postorbitals that approach each other behind the pineal opening and form a ridge, small downwardly and forwardly directed tusk, broad and deep front portion of the lower jaw, and the very small intramandibular foramen.

Diictodon ictidops (Broom, 1913)

Dicynodon ictidops Broom, 1913: 466, figs 5–6.

Pylaecephalus ictidops (Broom, 1913) van Hoepen, 1934: 93.

Diictodon ictidops (Broom, 1913) Cluver & Hotton, 1981: 130.

The holotype, AMNH 55110, is a skull from Beaufort West commonage, Cape Province, South Africa (*Cistecephalus* bio-zone according to Kitching 1977).

Broom (1913) described a number of small skulls from the same locality as being narrow with large, rounded nostrils. He noted that the septomaxilla does not show on the side of the skull and that the tusks are variably expressed, being absent in at least one specimen. The zygomatic arch beneath the postorbital bar was described as being very deep. Broom noted that the preparietal does not surround the pineal foramen.

Diictodon palustris (Broom, 1913)

Emydorhynchus palustris Broom, 1913: 456, fig. 19.

Diictodon palustris (Broom, 1913) Cluver & Hotton, 1981: 130.

The holotype (AMNH 5512) is a skull from New Bethesda, Graaff-Reinet District, Cape Province, South Africa. This is in the *Daptocephalus* bio-zone (Kitching 1977).

Broom (1913) noted the short preorbital part of the skull, the absence of tusks, the apparent absence of the septomaxilla (or its reduction), the large preparietal, and the large postorbital, which was considered to be unusual in that it was broad in front and narrow posteriorly.

Diictodon testudirostris (Broom & Haughton, 1913)

Dicynodon testudirostris Broom & Haughton, 1913: 36.

Pylaecephalus testudirostris (Broom & Haughton, 1913) van Hoepen, 1934: 93.

Diictodon testudirostris (Broom & Haughton, 1936) Cluver & Hotton, 1981: 130, figs 22–26.

The holotype, SAM–2354, is a skull from Dunedin, Beaufort West District, Cape Province, South Africa, a locality in the *Cistecephalus* bio-zone (Kitching 1977).

Distinguishing characters noted by Broom & Haughton (1913) are the very short beak, the maxilla which almost reaches the orbit, the apparent absence of the septomaxilla, the reduced lachrymal and prefrontal, the large postorbitals that meet in the midline, the large preparietal almost entirely in front of the pineal opening, the quadratojugal that is not ankylosed to the quadrate.

Diictodon sollasi (Broom, 1921)

Dicynodon sollasi Broom, 1921: 648, figs 28–29.

Pylaecephalus sollasi (Broom, 1921) van Hoepen, 1934: 93.

Diictodon sollasi (Broom, 1921) Cluver & Hotton, 1981: 132.

The holotype (SAM–7420) is from Biejiespoort, Victoria West District, Cape Province, South Africa, in the *Cistecephalus* bio-zone according to Kitching (1977).

Broom's (1921) description was based on many skulls from the same locality. He noted that immediately behind the plane of the nostrils there is a thickening of the bones, which forms a low, round, button-like boss in the midline. Other features to which attention was drawn were the canine that had a thickened ridge above and behind it, and the small preparietal. Broom (1921) distinguished *Dicynodon sollasi* from other species on the basis of such characters as the delicate build of the skull, the feeble tusk, the degree to which the postorbitals overlap the parietals, and the size of the preparietal.

Diictodon haughtonianus (von Huene, 1931)

Dicynodon haughtonianus von Huene, 1931: 30, fig. 25.

Diictodon haughtonianus (von Huene, 1931) King, 1988: 121.

The holotype (UT Von Huene 1931 Abb 25) is a skull and anterior part of lower jaw from Bloukrans, Prince Albert, South Africa, in the *Tapinocephalus* bio-zone (Kitching 1977).

Von Huene (1931) distinguished this species from others by its smaller nasal opening which lies further from the maxillary rim, the caniniform process which is more backwardly directed, the delicate postorbital bar, the shorter and wider postfrontal, and the shape of the preparietal.

Diictodon rubidgei (Broom, 1932)

Dicynodon rubidgei Broom, 1932: 189, fig. 62.

Pylaecephalus rubidgei (Broom, 1932) van Hoepen, 1934: 93.

Diictodon rubidgei (Broom, 1932) Cluver & Hotton, 1981: 133.

The holotype (BMNH 47081) is a skull from the Graaff-Reinet commonage, Cape Province, South Africa. This is in the *Cistecephalus* bio-zone (Kitching 1977).

Broom (1932) did not specifically allude to any distinguishing characters, but he mentioned the large preparietal and small pineal opening, and the large postfrontal. He noted that the postorbital is moderately large but its junction with the squamosal is not as far back as in most species of *Dicynodon*.

Diictodon grimbeeki (Broom, 1935)

Dicynodon grimbeeki Broom, 1935: 7, figs 6-7.

Diictodon grimbeeki (Broom, 1935) Cluver & Hotton, 1981: 133.

The holotype (TM 253) is a skull from Leeuwpoot, Beaufort West District, Cape Province, South Africa. The locality is in the *Cistecephalus* bio-zone (Kitching 1977).

Broom (1935) described a sample of 19 skulls from the locality and noted that the morphology of the preparietal varies within the sample. A small boss behind the pineal foramen was noted, as was the smooth rounded median boss on the snout formed by the nasals and the premaxilla. Broom distinguished male and female skulls, noting that the male skulls are bigger than those of the females, due to the much larger snouts of the former. The males were considered to have tusks; the females no or rudimentary tusks.

Diictodon nanus (Broom, 1936)

Dicynodon nanus Broom, 1936: 379, fig. 25A.

Diictodon nanus (Broom, 1936) Cluver & Hotton, 1981: 133.

The holotype (TM 268) is a skull from Houd Constant, Graaff-Reinet District, Cape Province, South Africa, in the *Cistecephalus* bio-zone (Kitching 1977).

Broom considered this to be a juvenile form. He noted the complete absence of postfrontals, that the postorbitals do not meet over the parietals, and that a developing canine (or possibly postcanine) is present behind the feebly developed caniniform processes.

Diictodon huenei (Broili & Schröder, 1937)

Dicynodon huenei Broili & Schröder, 1937: 130, figs 1–4 (preoccupied).

Dicynodon broilli (Broili & Schröder, 1937) Boonstra, 1948: 57.

Oudenodon huenei (Broili & Schröder, 1937) Toerien, 1953: 97.

Anomodon huenei (Broili & Schröder, 1937) Keyser, 1975: 74, fig. 28.

The holotype (BSP 1934 VIII 46) is a skull from La-de-da, Beaufort West District, Cape Province. The locality is in a high horizon of the *Tapinocephalus* bio-zone (Kitching 1977).

The main distinguishing features of this form mentioned by Broili & Schröder (1937) are its small size (total skull length 75 mm), the broad intertemporal and interorbital regions, the low bosses over the nostrils, the flat skull roof, the well-developed postfrontals, the large preparietal, the postorbital incompletely covering the parietals, and the beak-like dentary symphysis.

Diictodon broomi (Broili & Schröder, 1937)

Dicynodon broomi Broili & Schröder, 1937: 132, figs 5–13.

Diictodon broomi (Broili & Schröder, 1937) Cluver & Hotton, 1981: 134.

The holotype (BSP 1934 VIII 47a and b) comprises two skulls, one tusked, one tuskless from La-de-da, Beaufort West District, Cape Province. The locality is in a high horizon of the *Tapinocephalus* bio-zone (Kitching 1977).

The main distinguishing features of the species mentioned by Broili & Schröder (1937) are the skull (length 91 mm), which is slightly larger than that of the other specimens described in the same paper, the strongly developed preorbital region of the skull with a median boss between the nasal openings, the interorbital distance which is slightly broader than that of the intertemporal, the flat skull roof, the pineal foramen surrounded by a ring of bone, the large tusk, and the postorbitals which converge behind the pineal opening, covering the parietals.

Diictodon grossarthi (Broili & Schröder, 1937)

Dicynodon grossarthi Broili & Schröder, 1937: 161, figs 14–18.

Diictodon grossarthi (Broili & Schröder, 1937) Cluver & Hotton, 1981: 134.

The holotype (BSP 1934 VIII 48) is a skull from La-de-da, Beaufort West District, Cape Province, in a high horizon of the *Tapinocephalus* bio-zone (Kitching 1977).

The main distinguishing features mentioned by Broili & Schröder (1937) are the delicate snout, the convex skull roof, the absence of tusks, the low median boss over the nostrils, the delicate postorbital bar, the palatine which reaches relatively far forward on the palate, and the oval depression at the junction of the ectopterygoid, jugal and palatine.

The skull length is approximately 100 mm.

Diictodon aneae (Broom, 1940)

Dicynodon aneae Broom, 1940: 181, fig. 23.

Dicynodon whitsonae Toerien, 1954: 937.

Diictodon whitsonae (Toerien, 1954) Cluver & Hotton, 1981: 134.

Diictodon aneae (Broom, 1940) comb. nov.

It should be noted that Toerien (1954: 937) renamed this species *Dicynodon whitsonae*, believing that *Dicynodon anaeae* was preoccupied by the Russian form described by Amalitsky (1922) as *Dicynodon anaeae*. Cluver & Hotton (1981: 134) followed Toerien's species reassignment and, in addition, referred *Dicynodon whitsonae* to *Diictodon*. King (1988) also accepted *Diictodon whitsonae* as the valid species. However, these authors failed to notice that the spelling of Broom's original species, *anaeae*, was distinct from that of the Russian form, *anaeae*. The original species name given by Broom (1940) is therefore valid. It is here referred to the genus *Diictodon* as *Diictodon anaeae*.

The holotype (RC 42) is a skull from Wellwood, Graaff-Reinet District, Cape Province, South Africa. The locality is in the *Cistecephalus* bio-zone (Kitching 1977).

The only noteworthy feature of this small tusked specimen from Broom's (1940) description is the fact that the postorbitals are well developed, but the posterior processes are shorter than in most species.

Diictodon pseudojouberti (Boonstra, 1948)

Dicynodon pseudojouberti Boonstra, 1948: 60.

Diictodon pseudojouberti (Boonstra, 1948) Cluver & Hotton, 1981: 134.

The holotype (SAM-774) is a skull from Prince Albert Road, Cape Province, South Africa, in the *Tapinocephalus* bio-zone (Kitching 1977).

From Boonstra's (1948) description, the points of distinction of this species appear to be the relatively high and fairly broad skull, the fairly weak snout, the interorbital width being approximately equal to the intertemporal, the convex intertemporal and interorbital regions, the large and roughly oval preparietal, the well-developed postfrontal, and the postorbitals that are large and overlap the parietals.

Diictodon vanderhorsti (Toerien, 1953)

Dicynodon vanderhorsti Toerien, 1953: 91, fig. 60.

Diictodon vanderhorsti (Toerien, 1953) Cluver & Hotton, 1981: 135.

The holotype (BPI 175) is a skull from Antjiesfontein, Prince Albert District, South Africa, in a low horizon of the *Tapinocephalus* bio-zone (Kitching 1977).

Toerien (1953) noted that a low boss is present over the nostrils, and a low bony ring surrounds the pineal foramen. He discussed variation within dicynodonts and suggested that replacement canines are only found in young individuals, that nasal bosses increase with the size of the individual, and that the pineal boss is characteristic of old males.

Diictodon tienshanensis (Sun, 1973)

Dicynodon tienshanensis Sun, 1973: 56, figs 1-6.

Diictodon tienshanensis (Sun, 1973) Cluver & Hotton, 1977: 179, pls 73-74.

The holotype (IVPP V.3260) is a skull from the north foot of the Tianshan mountains, XinJiang Province, China. This is in the Upper Jijicao Group, perhaps equivalent to either the *Cistecephalus* or *Daptocephalus* bio-zone (King 1992).

Sun (1973) did not note any features of the skull that might distinguish this species from any other, apart from in the palate. Here the large interpterygoid fossa and long, narrow interpterygoid foramen are specified. In addition, Sun noted that the palatine forms a nodule at the anterior end, which projects internally and constricts the anterior end of the internal nares, and a small boss also projects at the inner posterior side of the maxillary process.

ASSESSMENT OF CHARACTERS

The features that previous authors have felt to be important in terms of recognizing the above species can be categorized as follows:

Features of the pineal and preparietal

- 1.1 Pineal foramen surrounded by a ring of bone
- 1.2 Pineal foramen situated on an elevated preparietal
- 1.3 Size and shape of the preparietal
- 1.4 Position of the preparietal relative to the pineal opening

General skull features

- 2.1 Skull roof flat, concave or convex
- 2.2 Height of skull
- 2.3 Breadth of skull
- 2.4 Narrowness of skull
- 2.5 Length of skull
- 2.6 Whether skull is robust or delicate
- 2.7 Width of occiput
- 2.8 Width of intertemporal region relative to skull length
- 2.9 Width of intertemporal region relative to interorbital
- 2.10 Length of preorbital part of the skull
- 2.11 Whether snout is delicate or robust

Features relating to the nasals and nostrils

- 3.1 Width of nasals
- 3.2 Size and shape of nostrils
- 3.3 Position of nostril relative to maxillary rim

Features of the postorbital bones

- 4.1 Whether and how far the postorbitals approach each other behind the pineal opening
- 4.2 Shape of the postorbital

Features of the caniniform process and tusks

- 5.1 Direction of the caniniform process or tusk
- 5.2 Presence and size of canine tusks

Features relating to skull bosses

- 6.1 Whether a boss is present behind the pineal foramen
- 6.2 Whether separate nasal bosses are present
- 6.3 Whether median boss over the nostrils is present

Features of the lower jaw

- 7.1 Whether the dentary symphysis is beak-like
- 7.2 Whether front part of lower jaw is broad and deep
- 7.3 Size of intramandibular foramen

Features relating to individual bones or specific areas of the skull

- 8.1 The septomaxilla does not show on the side of the skull
- 8.2 Presence, absence or reduction of the septomaxilla
- 8.3 Depth of the jugal arch
- 8.4 The prefrontal region of orbital margin is elevated
- 8.5 The frontal region is broad and flat
- 8.6 Maxilla almost reaches the orbit
- 8.7 The prefrontal is reduced
- 8.8 Quadrato-jugal not ankylosed to the quadrate
- 8.9 Whether the postorbital bar is delicate
- 8.10 Size and shape of the postfrontal

Features of the palate

- 9.1 The palatine reaches relatively far forward on the palate
- 9.2 Presence of an oval depression at the junction of the ectopterygoid, jugal and palatine
- 9.3 Size of interpterygoid fossa
- 9.4 Length and breadth of interpterygoid foramen
- 9.5 Whether a nodule is present on the anterior end of the palatine
- 9.6 Whether a small boss is present on the inner posterior side of the maxillary process

Several of these features may be dismissed at once, since it is now known that they do not constitute valid specific characters, either because they vary within otherwise similar forms, or because they are widespread among many different forms, or are likely to have been produced by distortion or bad preservation.

The size and shape of the preparietal and its position with respect to the pineal opening (1.3, 1.4) are examples of known variation within a group (Toerien 1953) and may be dismissed.

Features 2.1–2.5, 2.7, 2.8, 3.2, 5.1, 9.3, and 9.4 may all be affected by distortion and are therefore unreliable.

Features 8.1, 8.5, 8.6 and 8.7 occur in all specimens of *Diictodon* investigated. Feature 8.8 (quadratojugal not ankylosed to the quadrate) is now known to be the case in the majority of dicynodonts (see King 1981).

Feature 4.1 (whether and how far the postorbitals approach each other behind the pineal opening) varies within the group of species discussed above. The postorbitals usually approach each other in the midline but they do not always cover the parietals completely. Nevertheless, the 'pinched-in' appearance of the intertemporal bar seems to be a typical feature of *Diictodon*, as noted by Cluver & Hotton (1981).

Some features (2.6, 2.11, 8.9) are based on subjective non-quantitative assessments, e.g. the suggestion that the skull is delicate. Broom (1921) used this feature to distinguish between *Diictodon feliceps* and *Diictodon sollasi* but, in any case, the two skulls are of different sizes and it might be expected that the larger would be less delicate. I will not use these more subjective features further in the discussion.

The remaining features are discussed further below. I have used a sample of well-preserved and well-prepared specimens in the South African Museum (Appendix 1) to investigate the states of the features given above: to determine whether the features are identifiable consistently, how often they occur, and how much variation they exhibit.

Of the 37 skulls and jaws in this sample, two are from the *Tapinocephalus-Bradysaurus* assemblage zone, four from the *Pristerognathus-Diictodon*, three from the *Cistecephalus-Aulacephalodon*, two from the *Dicynodon-Theriognathus*, and the remainder from the *Tropidostoma-Endothiodon* assemblage zone. These numbers do not represent the abundance of specimens per stratigraphic zone in the field, nor probably in life, but reflect the composition of the collections available for study.

Pineal foramen surrounded by a ring of bone (1.1); and pineal foramen situated on an elevated preparietal (1.2)

Out of the South African Museum sample of 37 skulls, 15 specimens show some indication of a ring-like structure or bulbous area around the pineal foramen. (The latter seems to be what is meant by elevated preparietal in previous authors' descriptions of *Diictodon sesoma* and *Diictodon psittacops*.) The two conditions do not seem to be independent. In larger specimens the ring around the pineal opening becomes swollen, giving the bulbous or elevated structure.

It is possible that, in two specimens where the skull roof is slightly weathered, the ring may have been lost if it had been present but very slightly developed in the first place.

The presence of this structure does not correlate with any particular assemblage zone, the 16 specimens coming from the *Tapinocephalus-Bradysaurus* assemblage zone (1), the *Pristerognathus-Diictodon* assemblage zone (2), and *Tropidostoma-Endothiodon* assemblage zone (13). Specimens without the feature are also known from the *Tapinocephalus-Bradysaurus* and *Tropidostoma-Endothiodon* zones.

The feature correlates in some way with size, since the seven largest specimens (approximately 90–120 mm skull length) in the sample all have it, but in smaller specimens the feature may or may not be present. The smallest skull in the sample (skull length 47 mm) does not have the feature. The ring or bulbous area tends to be better developed in the larger specimens. Both tusked and tuskless specimens have the feature. Since this is a feature that may well be correlated with size of skull (as Toerien (1953) also pointed out), it is not a useful feature for delineating species.

Width of intertemporal region relative to interorbital (2.9)

Comments on the relative intertemporal and interorbital widths are made by previous authors for several species. This feature is dependent on the measurement of the intertemporal width, which is in turn dependent on how much the postorbitals overlie the parietals. This may be affected by distortion in two ways. The intertemporal region may be pinched together, forcing the postorbitals to approach each other more closely, forming ridges above the surface of the parietals. Secondly, it may be possible for post-mortem compression to cause the postorbitals to slide over the parietals, presumably either medially or laterally, reducing or increasing the intertemporal distance, respectively. The evidence for this is that some specimens in the South African Museum sample have a layer of matrix between the postorbitals and parietals, indicating that there must be space between the two bones. Because of this it is difficult to measure the true intertemporal width and use of this ratio as a specific character is not advisable, as Keyser (1975) pointed out.

Length of preorbital part of the skull (2.10)

There are two problems with using this feature for taxonomic purposes. The first is that it is not known how the preorbital part of the skull would be affected by distortion and whether it would react in the same way to compressive or tensional forces as the rest of the skull. If, for example, it were more resistant to compression, then preorbital/skull length ratios would be unreliable.

Secondly, Toerien (1953) gave evidence that the snout length increases relatively more quickly with increasing skull length, and so this may be another feature attributable to age difference.

Width of nasals (3.1)

Broom (1912) suggested that the nasals of *Diictodon psittacops* are so narrow that the nostrils face almost directly upwards. However, this is an unreliable character, since dorso-ventral flattening of the skull due to distortion would produce more upwardly-directed nostrils, and also the antero-dorsal margin of the nostril is very thin and may be worn away, making the nasals narrower.

Position of nostril relative to maxillary rim (3.3)

This feature will be affected by distortion and preservation. If the skull is subject to antero-posterior compression, the snout becomes flattened posteriorly and the nostril appears to lie nearer the anterior surface of the skull. If the maxillary rim of the snout is worn away, the nostril will appear to be nearer the ventral maxillary rim. Wearing away of the maxillary rim is not always obvious, since the rim is thin and the bone has an unfinished appearance and does not always show a break cleanly.

Whether and how far the postorbitals approach each other behind the pineal opening (4.1)

The tendency for the postorbitals to approach each other in the dorsal midline, covering the parietals in the intertemporal region has been used as a diagnostic character for *Diictodon* (Cluver & Hotton 1981; Cluver & King 1983). Although this tendency is present, the degree to which the postorbitals cover the parietals is variable. As mentioned under 2.9, the intertemporal region may be affected by distortion such that the configuration of the postorbitals changes. Because of this the degree to which the postorbitals meet each other over the parietals should not be given undue emphasis.

Shape of the postorbital (4.2)

Broom (1913) noted that the postorbital in *Diictodon palustris* differs in shape from anything known in dicynodonts, being so broad in front as to roof over part of the temporal fenestra, but narrowing rapidly behind. This condition is seen in other specimens (SAM-K7673, SAM-K7674), where it would appear that the thinner medial part of the postorbital behind the pineal opening has broken off on both sides. This gives the appearance of the postorbital narrowing posteriorly.

Presence and size of canine tusks (5.2)

Various conditions of the caniniform tusks have been noted by previous authors (Broom 1905, 1913, 1921, 1935; Broili & Schroder 1937; Toerien 1953). They have been

reported to be large or small, always present, always absent, or variably present within the same alleged species. In the latter case authors have explained this by sexual dimorphism and/or ontogenetic variation.

The question of sexual dimorphism in dicynodonts, as evidenced by presence or absence of tusks, is a long-standing one. It was reviewed by Cluver (1971), but it was not then possible to draw any conclusions. As far as *Diictodon* is concerned, data given by Smith (1989) are highly suggestive that sexual dimorphism is present in this genus, one sex being tusked, the other tuskless. In a collection of skulls from one locality (Dunedin, Beaufort West), Smith noted that 94 specimens were tusked, 84 tuskless and the condition of 18 could not be deduced from the material at that stage.

If several *Diictodon* skulls were to be reported from one locality and horizon all either with or without tusks, then presence and absence of tusks could be used as a valid feature of a species. However, this is not true for any of the hitherto recognized species of *Diictodon*. It is far more likely that the condition of the tusks is a sexually dimorphic or ontogenetic feature and, therefore, it should not be used to distinguish different species.

Whether a boss is present behind the pineal foramen (6.1)

Only one species, *Diictodon grimbeeki*, is reported to have a boss behind the pineal region. In his description of the species, Broom (1935) mentioned 19 'fairly good skulls', but does not say how many of them have a post-pineal boss.

The feature occurs in one specimen in the South African Museum sample, SAM-K7132. The latter specimen is tusked, approximately 115 mm in skull length (the largest in the collection), and is from the locality Leeukloof in the *Tropidostoma-Endothiodon* assemblage zone of South Africa. The type of *Diictodon grimbeeki* is from the same locality. Both tusked and tuskless forms were reported by Broom (1935). The type skull is 120 mm in length.

Several other *Diictodon* specimens in the South African Museum sample are known from this locality, but none has a post-pineal boss. These specimens are otherwise indistinguishable from the specimen with the post-pineal boss. There is evidence that other kinds of dicynodont skull bosses (nasal, frontal, pineal) are correlated with size or sexual dimorphism (Toerien 1953; Tollman *et al.* 1981) and it is most likely that the occasional occurrence of a post-pineal boss also falls within the category of intraspecific variation of some kind.

Whether separate nasal bosses are present (6.2); and whether a median boss over the nostrils is present (6.3)

Separate nasal bosses are present in *Diictodon heuneii* and a single median boss in various other species. All specimens in the South African Museum sample have nasal bosses of some description, but it is often difficult to say whether they are separate or confluent. For example, they may be separated from each other medially, but confluent posteriorly. Separation also depends to some extent on how well developed the bosses are, and on distortion of the snout.

Whether the dentary symphysis is beak-like (7.1)

The degree to which the dentary symphysis appears beak-like depends on how well the front end of the lower jaw is preserved, and is an unreliable character.

Whether the front part of lower jaw is broad and deep (7.2)

In order to be applicable to other specimens, this feature needs quantifying: the breadth and depth in question need to be related to some other aspect of jaw size, such as length. However, such measurements are prone to distortion and affected by incomplete preservation. Therefore in many cases they would simply be estimates, so the feature is likely to be unreliable.

Size of intramandibular foramen (7.3)

This feature is affected by distortion. The fenestra may appear to be closed-up if the spur of the dentary, which runs dorsal to the fenestra, is pushed downwards over it. The fenestra may appear to be of very different sizes on the opposite sides of a single jaw (e.g. SAM-K7738) if distortion has affected them differently.

Presence, absence or reduction of the septomaxilla (8.2)

It has been suggested that the septomaxilla may be absent or reduced in two species, *Diictodon palustris* (Broom 1913) and *Diictodon testudirostris* (Broom & Haughton 1913). Broom (1913) stated that, 'There does not appear to be a septomaxillary. If one is present it is very small and does not show on the face.' Broom & Haughton (1913) were similarly unsure, 'There is no evidence of a septomaxillary, at least on the outer side of the skull. Whether there may be one hidden underneath it is impossible to say without damaging the skulls. We incline, however, to think that the septomaxillary is absent.'

The septomaxilla is a small, fairly loosely-articulated bone, which is probably easily lost from the skull, as noted by Cluver & Hotton (1981) in *Diictodon galeops*. Its absence in the fossil does not necessarily mean it was absent in life. Well-preserved and well-prepared specimens in the South African Museum sample invariably show a septomaxilla, although it is often broken and never appears on the face.

Depth of the jugal arch (8.3)

Both *Diictodon ictidops* and *Diictodon jouberti* are noted as having a very deep zygomatic arch beneath the postorbital bars. However, this is a feature that may be produced by deformation of the skull. Two skulls in the South African Museum sample illustrate this. SAM-K7738 has been dorso-ventrally compressed and the zygoma lies more horizontally than usual. In side view this gives the impression of a shallow zygoma. SAM-K7281 has been laterally compressed and the zygoma lies almost vertically and appears very deep. The type of *Diictodon jouberti* is damaged in the zygomatic region but the skull has been compressed laterally and there is a break between zygoma and post-orbital bar. The type of *Diictodon ictidops* is described as narrow so there is also the possibility that it has been laterally compressed.

This is clearly an unreliable feature on which to base specific distinction.

The prefrontal region of orbital margin is elevated (8.4)

Broom (1912) noted this feature in *Diictodon psittacops*, referring to thickening of the antero-dorsal margin of the orbit. A swelling in this position is present in many specimens and is particularly well developed in SAM-K7643, one of the largest individuals known. It is probably size related and unhelpful as a specific character.

Size and shape of the postfrontal (8.10)

Various sizes and shapes of the postfrontal have been described in type specimens. The bone was said to be short and wide in *Diictodon haughtonianus*, absent in *Diictodon nanus* and *Diictodon galeops* and fairly well-developed in *Diictodon pseudojouberti*, large in *Diictodon rubidgei*, and clearly present in *Diictodon huenei*. The South African Museum sample also shows that the bone is very variable both in size and shape. It may be a fairly well-developed triangular bone that reaches the orbital border, or a mere sliver of bone confined to the skull roof. Conditions in between these extremes can be seen. It seems unwise to use this character to separate species because of its great variability.

The palatine reaches relatively far forward on the palate (9.1)

Although there is some variability in the sutural pattern in *Diictodon*, the typical pattern (as seen in the South African Museum sample specimens) is for the maxilla to separate palatine and premaxilla (see Fig. 2). The palatine bone does not usually run anteriorly to contact the premaxilla as it does in *Diictodon grossarathi*. This seems then to be a distinctive feature of *Diictodon grossarathi*. The type is from the locality La-de-da in the *Pristerognathus-Diictodon* assemblage zone, as are the types of *Diictodon huenei* and *Diictodon broomi*, which are otherwise very similar but do not exhibit this particular condition of the premaxilla. SAM-K7643 from La-de-da also shows a sutural pattern within the normal range of variation for other *Diictodon* specimens.

In the South African Museum sample, the degree to which the palatine approaches the premaxilla is variable but nothing like the condition illustrated in *Diictodon grossarathi* occurs. Although it is possible that this might represent a real difference between *Diictodon grossarathi* and other specimens, in view of its occurrence in only one known specimen, and the variability of the sutural pattern in other specimens, it should not be regarded as a reliable specific character.

Presence of an oval depression at the junction of the ectopterygoid, jugal and palatine (9.2)

This feature was noted in *Diictodon grossarathi* by Broili & Schröder (1937). It occurs in many, but not all, of the specimens of the South African Museum sample, although its size is variable. It does not seem to be helpful in distinguishing separate species, because of its wide variability.

Whether a nodule is present on the anterior end of the palatine (9.5)

This feature is noted by Sun (1973) in *Diictodon tienshanensis*, a tuskless specimen. It is present also in specimens of the South African Museum sample, both tusked and tuskless, where preservation of the palatine is good. It is probably a constant feature of the genus and not of use in delineation of species.

Whether a small boss is present on the inner posterior side of the maxillary process (9.6)

This is another feature noted by Sun (1973) in *Diictodon tienshanensis*. Most specimens of the South African Museum sample have a small tubercle behind the canine tusk or flange, although in some cases this is very indistinct. A similar tubercle was noted by Cluver (1970) in *Diictodon testudirostris*. Again this feature is probably present throughout the genus and not of help in delineation of species.

SUMMARY

None of the various features used by previous authors seems acceptable as characters on which to base specific differences. However, with a sample of fossils that are adequately preserved and prepared, it might prove possible to find other features not noted by previous authors owing to indifferent specimens or incomplete preparation. The South African Museum sample was studied from this point of view, but no obvious candidates were found. Although there is variability in the sample in features such as preparietal suture, premaxilla suture, bosses, and canine tusks, none of these is useful for delimiting species, as discussed above.

CONCLUSION

Since no reliable specific characters can be found, it is not possible to justify the 20 different species of *Diictodon* that exist in the literature. There is no reason why all *Diictodon* specimens should not be referred to *Diictodon galeops*.

Diictodon galeops is distinguished by the generic features of *Diictodon*: dicynodonts that are tusked or tuskless, have a narrow intertemporal region with the postorbitals tending to cover the parietals behind the pineal foramen, although this covering is not always complete. The pineal foramen is often surrounded by a bony ring or boss, especially in larger specimens. The intertemporal region is approximately the width of the interorbital region. There are bosses over the nostrils, which are sometimes confluent in the midline. The caniniform process (whether bearing a tusk or not) is set obliquely to the ventral maxillary rim, leaving a sharp-edged notch. The premaxilla and palatine are separated by the maxilla on the palatal surface. The palatine bears a small boss on its antero-medial corner. The maxilla bears a small tubercle postero-medial to the caniniform process. The anterior rami of the pterygoid are straight and built up into strong keels midway along their length. There are two anterior palatal ridges that meet the anterior premaxillary margin, a single median premaxillary ridge, and low ridges running along the maxilla-premaxillary suture.

The lower jaw has distinctive dentary tables that are excavated into shallow troughs and whose medial edge is higher than the lateral. The postero-medial corner of the dentary table is drawn out into a distinct angle overhanging the edge of the jaw ramus. The lateral dentary shelf is not prominent.

As far as can be ascertained from specimens available for study, the genus *Diictodon* appears to contain only one justifiable species, *Diictodon galeops*. This species is thus known from the *Tapinocephalus-Bradysaurus* assemblage zone through to the *Dicynodon-Theriognathus* zone of the Late Permian Karoo sediments of South Africa. The genus is also known from Zambia (Gale 1988), China (Sun 1973), and Russia (pers. obs.). Although the precise correlation with the South African stratigraphic scheme is uncertain at present, the non-South African specimens of *Diictodon* are from rocks probably equivalent to *Cistecephalus-Aulacephalodon* or *Dicynodon-Theriognathus* assemblage zones, (King 1992), and they therefore fall within the known range of the genus in South African rocks.

One qualification about this range should be noted. Specimens of *Diictodon* from the *Tapinocephalus-Bradysaurus* assemblage zone are rare in museum collections, and often

very poorly preserved. (Several specimens in the South African Museum collections which were prepared in the hope that they were *Diictodon* in fact proved to be *Robertia* (King & Rubidge in press). It is possible that *Robertia* may well be the relatively common dicynodont in the *Tapinocephalus*–*Bradysaurus* assemblage zone, rather than *Diictodon*.) Therefore, while this study has attempted to use well-preserved and well-prepared specimens, this has been possible only to a lesser degree with *Tapinocephalus*–*Bradysaurus* assemblage zone specimens. However, specimens at my disposal, even when poorly preserved, show no difference in the general suite of characters used to define the genus, and exhibit no characters which might be used to delineate a species other than *Diictodon galeops*.

If *Diictodon* can be considered to span all but the lowest of the Late Permian assemblage zones of the Karoo, this would give it a species longevity of between five and ten million years, since Rubidge (in press) considers the *Tapinocephalus*–*Bradysaurus* assemblage zone to be between 258 Ma and 253 Ma and the *Dicynodon*–*Theriongnathus* assemblage zone to be Upper Tatarian (up to 248 Ma).

It appears that the one species, *Diictodon galeops*, is both long-lived and widespread. Since few specific revisions of mammal-like reptiles have been carried out so far, few measurements of specific longevity are available and this information on *Diictodon* will therefore make a useful contribution to discussions of species longevity and diversity in the Late Palaeozoic.

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REFERENCES

- AMALITSKY, V. 1922. Diagnoses of the new forms of vertebrates and plants from the Upper Permian of North Dvina. *Bulletin of the Academy of Sciences of St Petersburg* **16** (6): 329–340.
- BOONSTRA, L. D. 1948. Anomodont reptiles from the *Tapinocephalus* zone of the Karoo System. In: DU TOIT, A. L. ed. *Special Publications of the Royal Society of South Africa. Robert Broom Commemorative Volume: 57–64*. Cape Town: Royal Society of South Africa.
- BROILI, F. & SCHRÖDER, J. 1937. Beobachtungen an Wirbeltieren der Karrooformation. XXVIII. Über einige neue Anomodontier aus der *Tapinocephalus*-Zone. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften zu München* **1937**: 118–168.
- BROOM, R. 1905. Notice of some new fossil reptiles from the Karroo Beds of South Africa. *Records of the Albany Museum* **1** (5): 331–337.
- BROOM, R. 1912. On some fossil reptiles from the Permian and Triassic beds of South Africa. *Proceedings of the Zoological Society of London* **1912** (2): 859–876.
- BROOM, R. 1913. On some new genera and species of dicynodont reptiles, with notes on a few others. *Bulletin of the American Museum of Natural History* **32** (26): 441–457.
- BROOM, R. 1921. On some new genera and species of anomodont reptiles from the Karroo beds of South Africa. *Proceedings of the Zoological Society of London* **1921** (2): 647–674.
- BROOM, R. 1932. *The mammal-like reptiles of South Africa*. London: H. F. & G. Witherby.
- BROOM, R. 1935. A new genus and some new species of mammal-like reptiles. *Annals of the Transvaal Museum* **18** (1): 1–12.